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REPEATED FLOWERING OF INTRODUCED PLANTS

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REPEATED FLOWERING OF INTRODUCED PLANTS

/Following is a translation of a Russian language article by B. N. Golovkin and G. N. Andreyev, Polar-Alpine Botanical Garden, USSR Academy of Sciences, city of Kirovsk, which was submitted on 26 April 1961. It appeared in Botanical Journal No 1, 1963, pp 113-118. Translation performed by Sp/6 Charles T. Ostertag Jr./

In the summer of 1960 in the Polar-Alpine Botanical Garden (Murmansk Oblast) unusually frequent secondary flowering of introduced plants was observed. While in 1959, secondary flowering in 17 species (19 specimens) was registered in the nurseries of the Garden, in 1960 plants of 53 species (70 specimens) bloomed a second time, or almost 5% of the herbaceous plants in the collections.

The abundance of incidents of secondary flowering undoubtedly was connected with the peculiarities of the growing season of 1960. The vegetation of plants in the nurseries began in the end of April or the beginning of May, that is 15-20 days earlier than is usual for the conditions of the Garden. In the beginning of the third decade of May a late spring frost of down to -7.8° hit unexpectedly and June continued cool. July on the contrary was of a rare sultry and arid weather, and August was comparatively warm and humid.

The basic feature of secondary flowering is the appearance of blossoms with the presence of ripe or almost ripe fruits from the first flowering. Secondary flowering was established more rarely when the fruits hadn't set, but after a yellowing of the generative and sometimes even the vegetative parts of the plants. A similar case with Rhodiola asiatica D. Don will be considered below.

The first plants which flowered for the second time were observed in the end of July, the high point of secondary flowering occurred in the second or third decade of August. The majority of plants (41 species or 77% and 45 specimens or 64%) began secondary flowering after ripening of the seeds. Not one specimen, except Draba from Tiksi (a city or town on the northern coast of the USSR near the mouth of the Lena River), produced secondary fruit bearing. Plants of 11 specimens (21%) after the first flowering generally didn't set the seeds, that is both flowerings were sterile. In 1959, 10 species (58%) comprising 12 specimens (63%) bloomed a second time after seeding and plants of 5 specimens (26%) didn't set the seeds after the first flowering.

In Silene acaulis L. from the Samoans, the secondary flowering in 1959 was more abundant than the first, but none of them turned out

to be fertile. In the summer of 1960 three flowerings were observed in Myosotis asiatica Schischk. et Serg., Cardamine hyperborea Schulz, and various species of the genus Draba.

There is comparatively little literary data on the secondary (or, more correctly, repeated) flowering of plants though this phenomenon is observed quite often in nature, especially in the South of the European part of the USSR (Illichevskiy, 1937).

It is possible that this phenomenon is natural also to the northern flora to no lesser degree. In the fall of 1958 we had noted secondary flowering in more than 30 species of plants in the tundra habitats of Chukotka and north of Yakutiya. Under the conditions of the Khibini Mountains, secondary flowering is observed almost yearly in a number of local plants (Phyllodoce coerulea Bab., Oxytropis sordida Willd., Rubus chamaemorus L.).

Repeated flowering occurs most often in herbaceous plants, less seldom in shrubbery, and is particularly rare in trees (Galakhov, 1937). Sometimes three and more outbreaks of flowering are observed in the course of a summer in one and the same plant. Thus, according to S. O. Illichevskiy (1937) in the summer of 1936 there were four flowerings in some apple trees. Repeated flowering in plants is usually observed during the humid and warm period at the end of summer. The positive influence of increased temperature and humidity is also noted in hothouse observations of the tropical shrubs Callistemon (Polunina, 1957; Kazaryan, 1959) which had bloomed a second time. Therefore many authors consider that repeated flowering is the result of the reaction of increased fall temperatures in conjunction with a high humidity which in the fall creates a repetition of spring conditions enabling the blossoming of the generative buds which were formed (Illichevskiy, 1925; Galakhov, 1937; Kazaryan, 1959; Voroshilov, 1960), especially if this was preceded by a very dry period (Galakhov, 1961).

There is information of various species of the genus Draba which were transferred from Greenland into Denmark acquiring the capability to bloom several times a year, which wasn't observed in the native land of these plants.

In the same experiment there was noted in Potentilla nivea L. perpetual blossoming which is unnatural for it, and Greenland willows shed and unfolded their foliage anew several times during the summer (Sorensen, 1941).

In literature there are indications of structural differences of shoots and flowers of secondary blossoming of woody varieties (Korovin and Tychiyev, 1948) and shrubs (Shteynberg, 1936). Such differences are also observed in herbaceous plants.

During the time between the beginning of secondary flowering and the end of vegetation, depending on low temperatures or snow fall, the plants usually are not able to form normally developed flowers or racemes. In the majority of cases the floral shoot is partially developed. It is often 1.5 - 2 times shorter than during the first flowering, the stems are correspondingly thinner and the stem leaves are smaller (figures 1 and 2). Most often a reduced number of flowers is observed on the stem, but there are exceptions. This year for example, in Campanula tridentata Schreb., which in nature has a single flowering floral stem, there was observed in late examples and in those blooming for a second time up to five normally developed flowers on a floral stem. Each flower was seated on a short peduncle coming out of the base of a stem leaf (figure 3).

Flowers during the period of secondary blossoming are on the average of approximately 1.5 times smaller than normally developed flowers, occasionally they are of the same size.

The structure of the generative shoot of Anemone crinita is interesting. Usually the raceme in this species under natural conditions is a simple 3-5 flowering umbel on a stem 12-45 cm in height. Under conditions at the Garden the number of flowers in the raceme is often increased to 6-7 and the height of the stem may reach 60 cm.

During secondary flowering a noticeable lag is observed in the development of certain flowers in the raceme in comparison with others. In one case proliferation of the raceme, continued growth of its rachis, and the formation of a secondary umbel were noted, at the same time in the lower umbel along with the normally developing flowers accessory rachises were formed, each of which bore a partially developed raceme (figure 4). Branching of the floral stem of Anemone crinita was observed even earlier, in 1957, when on the stem of a late flowering specimen a stem leaf was formed similar in form to radical leaves but somewhat smaller in size. From its base there emerged on a very long stem a "raceme" consisting of one flower with the small bracts of a spathe (figure 5).

It is necessary to add that neither the branching of stems nor the formation of stem leaves in Anemone crinita is observed in nature. All the structural changes of the generative parts were observed in plants that reproduced locally.

The proliferation of a flower during secondary flowering, emerging in the summer of 1959 in Adonis vernalis L. and A. sibiricus Patr., had the semblance of secondary growth. On one plant was found a partially developed flower, around 1.5 cm in diameter and in which parts of the floral envelope had turned green, which was little different from the whorls of the stem leaves following it. On other specimens, signs of

a flower weren't observed yet but there was a sharply limited zone of junction of the old dark green part of the stem and the light green foliated shoot 1.5 - 2.3 cm in length which developed from the flower bud. Apparently in the stage where the parts of the flower are differentiated, the generative bud was subjected to the influence of unfavorable external conditions which caused first, partial development, and then the proliferation of the flower. It must be added that in all the years, plants of the adonises referred to bloomed and bore fruit regularly and secondary flowering was observed only in 1939. A similar "secondary branching" was observed in 1960 in Thalictrum speciosissimum Loebl. from Upsala. Besides this, in Callianthemum angustifolium Witasek in August 1960 a repeated opening of the vegetative buds and the growth of young leaves took place (secondary flowering of this species was observed in only one specimen that was reproduced locally).

Digressing from the above described morphological and phenological anomalies of secondary flowering, all of its various forms may be converged into two types.

1. Late flowers appear in the bases of stem leaves which are setting on the floral stem left from the first flowering and in relation to the first axial flower or raceme are lateral (figure 6). Such a secondary flowering is in Aster alpinus L. This species in nature in a wild state blossoms with solitary calathides. In garden practice, sorts are encountered (for example A. alpinus superbus) with two or three racemes (Bailey a. Bailey, 1949). The position of these racemes on the stem is the same as described above, but usually the lateral racemes develop simultaneously with the axial racemes. We observed that the axial racemes appeared in 26 days after the blossoming of the raceme on the main rachis and in this manner a break in blossoming was formed.

In Ranunculus caucasicus M. B. blossoming on the lateral rachises began after the main rachis (in its upper portion) and the part of the plant from the base of which the lateral rachis emerges have dried up.

2. During repeated flowering a separate generative shoot is formed from the base of a radical leaf (figure 7). The majority of cases of secondary flowering are related mainly to this type. As an example here it is appropriate to present a somewhat unusual case of flowering in Rhodiola asiatica D. Don.

The late spring frosts of May 1960 led to the dying of the buds of the flower buds which weren't yet successfully expanded. The majority of plants, which were deprived thusly of flower buds, didn't bloom in the summer of 1960. Rhodiola asiatica, in which the May frost had destroyed the entire part which was above ground and in the vegetative phase, began to sprout a month after the frost and in replacement

the first dead buds formed new ones. Such a flowering (9 Jul - 14 Jul) can also be considered as secondary since a considerable period of dormancy passed between it and the first "potential" flowering.

A single flowering in the course of one vegetative period, apparently, must be considered the immature type of flowering formed as a consequence of the differentiation of the year into favorable and unfavorable periods for flowering. The condition of relative dormancy extending from one flowering to another was developed historically as an adaptation for the endurance of unfavorable conditions during which the plant is preserved in the condition of one or another form of survival buds (the term "winter buds" is used only for plants of temperate latitudes).

In countries with a constantly humid and warm climate, the old type of flowering is preserved - continuous. In actuality in many plants of the tropics at any time of the year on one and the same specimen we encounter, along with the flowers, fruits from a previous flowering.

Such a type of flowering as a reversible feature but limited in time by the vegetative period, can be encountered also in plants of temperate latitudes, for example in Herniaria glabra L. (Voroshilov, 1945). It can also be observed among introduced plants of the Polar-Alpine Botanical Garden. Such plants are Viola altaica Ker-Gawl., Papaver nudicaule L., Bellis perennis L., and Hutchinsia alpina R. Br.

The severe conditions of the July polar drought in 1960 caused a considerable interruption in the flowering of several of these. This demonstrates to us one of the possible causes of the origination of secondary flowering in plants to which continuous flowering is natural. From this it follows that some plants which flower secondarily, apparently can return to flowering continuously with the help of the appropriate agrotechnique.

Most of all repeated flowering may be considered a partial return to perpetual flowering of plants in which, during the course of evolution, stable solitary flowering was developed during the vegetative period. In this, the various ability for repeated flowering in various species and even in specimens of plants shows how conservative the dormancy period formed in them is, and how unstable the plant is under external conditions which permit the blossoming of dormant buds. Such reversion, as it follows from what has been said above, usually appears during the onset of particularly favorable conditions at the end of summer and in the fall (increased temperature and humidity) or during the transfer of the plants into new conditions which are more favorable for growth and development. Figuring that secondary flowering in the overwhelming majority of cases doesn't

produce seeds, it should be considered as an example of the relative adaptability of the plants to the conditions of the external medium.

In the conditions of the Garden the most conservative group in relation to secondary flowering were the geophytes, mainly the bulbous ones. The only rhizomatous geophyte in which secondary flowering was observed was Polygonum carneum C. Koch.

Somewhat apart stands the problem concerning the repeated flowering in introduced ephemeras. The majority of annual grains (Bromus, Bromopyrum, and others) have, under the conditions of the Kola Peninsula, two sharply expressed generations of generative shoots. In individual cases the first generation of shoots is sterile, the second -- fertile and more sturdy (for example, in Cen-Asian specimens of Bromus scoparius L.). Among specimens of B. tectorum reproduced at various places, depending on the conditions of the year, it was possible to see all the transitions from single heading to repeated and continuous. Carrying on similarly are the annual ephemeras from other families: Koeleria linearis Pall. and various species of Malcolmia and Roemeria. The facts presented once again testify to the great lability and intraspecies heterogeneity of ephemeras.

There are no concrete morphological facts at our disposal on which to lean, therefore in explaining the reason for the emergence of secondary flowering the following three circumstances may be proposed.

1. All the buds by the end of the vegetative period of the preceding year were in various phases of morphogenesis. During similar tempos of development the floral shoots from some buds achieved blossoming sooner while others did later; they will then and there produce secondary flowering. Apparently we have such a case during the first type of secondary flowering (Aster alpinus L., Ranunculus caucasicus M. B.).
2. All the buds by the end of the vegetative period were at the same stage of morphogenesis. But some of the buds were cut off in their development under the influence of some kind of inhibiting factors in the period between the end of vegetation of the preceding year and the beginning of budding in that year. Such buds which were inhibited during their development may produce a primordium later for generative shoots which cause secondary flowering.
3. A less probable circumstance is when the generative bud could have undergone vernalization and developed before flowering in the same vegetation period, that is in the year of flowering. There are facts at our disposal that a large part of decorative perennials under the conditions of our Garden form their generative organs in

the summer preceeding flowering. The epheremas naturally have a place namely in this third circumstance.

Concrete data regarding the expressed proposals may be obtained only by a detailed morphological analysis of generative buds of various years.

Illustrations

Figure 1 (page 114). Repeated flowering in Anemone crinita Juz.
a - generative shoot of the first flowering; b - repeated flowering.

Figure 2 (page 115). Repeated flowering in Senecio aureus L.
a - generative shoot of the first flowering; b - repeated flowering.

Figure 3 (page 115). Repeated flowering in Campanula tridentata Schreb.

Figure 4 (page 116). Repeated flowering in Anemone crinita Juz.
a - specimen carrying a proliferous raceme.

Figure 5 (page 116). Formation of the second raceme in Anemone crinita Juz. during repeated flowering.

Figure 6 (page 117). Development of racemes of the secondary succession in Aster alpinus L. during repeated flowering.

Figure 7 (page 117). Repeated flowering of Phyteuma orbiculare L.
The formation of independent generative shoots from the bases of radical leaves.

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